AGRICULTURAL DIMENSIONS of GLOBAL CLIMATE CHANGE

8

CARBON DIOXIDE EFFECTS on PLANTS:
UNCERTAINTIES and IMPLICATIONS for MODELING CROP RESPONSE to CLIMATE CHANGE

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I. INTRODUCTION

Quantification of the direct physiological and yield response of plants to increased atmospheric CO_2 concentrations involves many assumptions that add to the uncertainty of economic forecasts regarding climate change. An assumption of a positive crop response to additional CO_2, a so-called "CO_2 fertilizer effect," can have a substantial impact on predictions of yield and economic welfare, and thus can influence policy decisions regarding resource management and international food security.

To account for the CO_2 effect, most crop models to date have incorporated optimistic multipliers or yield shifts, the magnitude of which are based on experiments conducted under controlled conditions with adequate water and nutrients, optimal temperatures, and nonexistent weed, disease, and insect pressures. Depending on the magnitude of the CO_2 fertilizer effect assumed in a crop model, climatic changes that inhibit growth may be compensated for, and forecasts can shift from damaging to favorable. Models are sometimes run with and without the CO_2 fertilizer effect for purposes of sensitivity analysis, but conclusions, publications, and recommendations are typically based on full realization of a strong positive crop response to elevated CO_2. This chapter explores the physiological complexities of this response in the context of likely environmental and economic constraints of the future, and offers specific suggestions for improving this aspect of crop models and subsequent economic welfare predictions.

II. PLANT PHYSIOLOGICAL RESPONSE TO CO$_2$

This section briefly discusses the basic mechanisms associated with the CO$_2$ fertilizer effect, including possible feedback mechanisms which make it difficult to scale up from individual leaf to whole plant and ecosystem level predictions.

A. Effects on Photosynthesis

Photosynthesis is the process in which CO$_2$ enters the plant through small openings in the leaves called stomates, is captured or "fixed" by photosynthetic enzymes, and is then converted into carbohydrates. When atmospheric CO$_2$ concentration goes up, more CO$_2$ will tend to enter the leaves of plants (i.e., photosynthetic rate increases) because of the increased CO$_2$ gradient between the leaf and air. Of even more importance is that an increase in external CO$_2$ concentration inhibits photorespiration, a process in which oxygen is absorbed and CO$_2$ released by the plant. At current atmospheric CO$_2$ levels, photorespiration can reduce the net carbon gain from photosynthesis by as much as 50% (Tolbert and Zelitch, 1983).

The biochemistry of photosynthesis differs among plant species and this greatly affects their relative response to CO$_2$. Most economically important crop and weed species can be classified as either a C3 or C4 type, the names referring to whether the early products of photosynthesis are compounds with three or four carbon atoms. In controlled experiments, the C3 species (including wheat, rice, soybean, most horticultural crops, and many weed species) tend to show significant gains in net photosynthesis from increased CO$_2$ because of photorespiration inhibition. In contrast, C4 plants (e.g., maize, sorghum, sugarcane, millet, and many pasture, forage, and weed species) show much less response to increased CO$_2$ due to a more efficient carbon assimilation process, Figure 8-1. The C4 plants obtain essentially no benefit from the CO$_2$ inhibition of photorespiration.

Table 8-1 shows the percent change in photosynthesis at 680 compared to 300–350 ppm CO$_2$ for several important crop species. These data are based primarily on experiments in which temperature, water, and nutrients were not limiting factors. The C3 crops listed had an average short term increase of 50% compared to 11.5% for the C4 species. The data in Table 8-1 also indicate that, regardless of photosynthetic pathway, the response is often much less when plants are acclimated to high CO$_2$ for at least one week prior to measurement (average long term increases of 25% and 5% for C3 and C4 species, respectively).
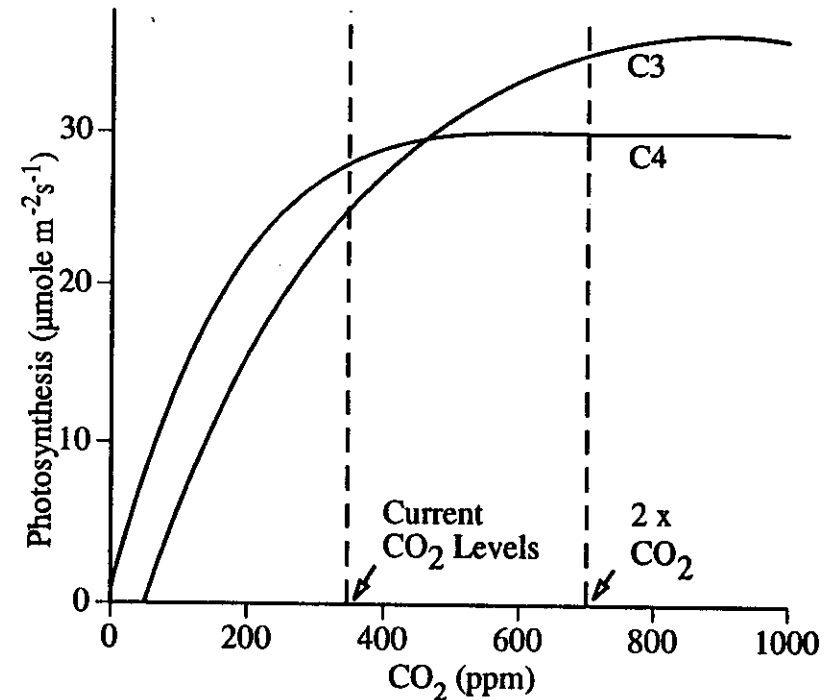

Figure 8-1. Photosynthesis per unit leaf area in relation to atmospheric CO$_2$ concentration. Typical curves for plants with the C3 and C4 photosynthetic pathway are compared. Although the specific photosynthetic values will vary among species, in general, C3 plants will show a greater relative benefit from a doubling of CO$_2$ compared to C4 plants.

B. Effects on Water Use By Plants

Another important direct effect of high CO$_2$ on plants is to cause a partial closure of the stomates. This restricts the escape of water vapor from the leaf (transpiration) more than it restricts photosynthesis. It is common for a doubling of CO$_2$ to decrease transpiration by 25–50 % (Cure and Acock, 1986). Water use efficiency (WUE), defined as the ratio of photosynthesis to transpiration, has been found to double with a doubling of CO$_2$ for some species (Pearcy and Björkman, 1983).

This stomatal response to CO$_2$ could moderate the increase in transpiration that is anticipated to occur with global warming, and could be of obvious benefit to plants growing under water-limited conditions. However, a more

Table 8-1. Photosynthectic response to CO_2-doubling for several crop species with either the C3 or C4 photosynthetic pathway.

Photosynthetic pathway	Crop	Percentage change in net photosynthesis after CO_2 doubling	
		Short term	Long term
C3	Barley	+50	+14
	Cotton	+60	+13
	Rice	+42	+46
	Soybeans	+78	+42
	Wheat	+41	+27
	Tomato	+30	+9
C4	Corn	+26	+4
	Sorghum	-3	+6

Note: Data are from several experiments and represent the percentage change at 680 ppm CO_2 compared with controls (300–350 ppm). Responses to short term and long term (>1 week) exposure to elevated CO_2 are presented.

Source: Yelle et al. (1989); Cure and Acock (1986).

efficient use of water per unit leaf area does not necessarily result in a reduction in total water requirements. The water savings benefit associated with partial stomatal closure can be counteracted entirely by larger plants with greater total leaf area (Rosenberg et al., 1990; Eamus, 1991). Allen et al. (1985), working with soybean, and Morison and Gifford (1984), comparing 16 crop species, found no difference in water use per plant between control and CO_2-enriched plants, although total plant leaf area was often greater in those grown at the higher CO_2 concentration.

A secondary effect of the stomatal closure response to increased CO_2 is to increase leaf temperatures, typically by 1–3°C (Idso et al., 1987; Jones et al., 1985). This occurs because there is less water evaporated at the leaf surface to cool it. A higher leaf temperature will increase the water vapor pressure within the leaf and *increase* transpiration. Also, if stomatal closure initially slows transpiration, humidity of the air surrounding the leaf becomes drier, which will tend to increase rather than decrease subsequent transpiration rates. These factors alone may counteract the water savings benefit from a CO_2 doubling (Jarvis and McNaughton, 1986).

C. Feedback Mechanisms and Acclimation to High CO_2

A major reason for uncertainty in predicting plant response to CO_2 is that physiological and morphological feedback mechanisms may limit the extent to which direct CO_2 effects are realized. The long term evolutionary response to higher CO_2 levels will also be very important, but little is known about this subject and it will not be addressed here.

i. Downregulation of Photosynthesis

The results in Table 8-1 indicate that the large increases in photosynthesis observed in short term experiments are seldom maintained when plants are exposed to high CO_2 for prolonged periods. Several explanations for this downward shift in photosynthesis, referred to as "downregulation," have been proposed. Many relate to the fact that, in the presence of high CO_2, the plant's ability to produce carbohydrates via photosynthesis may exceed the demand for carbohydrates in the remainder of the plant (Stitt, 1991). In some cases, excessive carbohydrates cause enlargement of starch grains within leaf cells, physically damaging organelles important in photosynthesis (DeLucia et al., 1985; Nafziger and Koller, 1976). Perhaps a more common mechanism is a feedback effect that reduces the activity of a key photosynthetic enzyme, Rubisco, by as much as 60% after prolonged exposure to high CO_2 (Sage et al., 1989).

A recent review (Stitt, 1991) concludes that the ability of a particular plant genotype to maintain photosynthetic rates at enhanced CO_2 levels will depend upon the supply-demand balance with regard to the products of photosynthesis (i.e., carbohydrates), and how this balance is regulated within the whole plant. Kramer (1981) suggested that indeterminate crop species, which have continued high demand for carbohydrates because they continue producing new fruit and leaves, respond more positively to increased CO_2 than determinate types.

ii. Leaf vs. Root and Fruit Growth

In general, how plants partition their biomass among leaves, roots, stems, seeds, and fruit has a tremendous impact on subsequent growth and yield and can easily overcome the influence of photosynthetic rate. A lack of correlation between photosynthesis and yield has long been recognized by plant breeders (Elmore, 1980). In terms of whole plant growth, the amount of leaf area available for light interception is just as important as photosynthesis per unit leaf area.

When considering the long term growth response in the field, shifts in biomass partitioning within the plant can have either a beneficial or negative effect, depending on environmental conditions. For example, an increase in leaf area due to high CO_2 would be of obvious benefit in terms of carbon- and energy-gaining ability, and could possibly compensate for the downregulation of photosynthesis phenomenon discussed above. However, large plants with greater leaf area will develop water and nutrient deficits more quickly if grown in a situation where these inputs are in limited supply.

The increase in root:shoot ratio sometimes observed at high CO_2 (Lawlor and Mitchell, 1991) may improve the ability to extract water and nutrients needed for growth, but if this occurs at the cost of reducing the amount of biomass allocated to the harvested portion of the plant, economic yield may be much less.

III. OPTIMUM YIELD RESPONSE TO CO_2 IN CONTROLLED ENVIRONMENTS

The preceding section described some of the reasons why an initial stimulation of photosynthesis due to enhanced CO_2 does not necessarily indicate an increase in yield potential. However, the experience in greenhouses and controlled environments has generally shown a benefit from additional CO_2, albeit less than the short term photosynthetic response, provided other growth conditions such as temperature, light, water, nutrients, air quality, and pest control are maintained near optimum. This information has formed the basis for quantification of the direct CO_2 effect as used in crop models.

A. Use of Supplemental CO_2 in Greenhouse Crop Production

It has been estimated that, worldwide, perhaps 50–75% of commercial greenhouses use some type of CO_2 enrichment to increase productivity (Wittwer, 1986). In The Netherlands, where the greenhouse industry is of considerable economic importance, this figure is closer to 80 or 90% for tomato, cucumber, sweet pepper, strawberry, and some flower and ornamental crops (Van Berkel, 1986). The widespread use of this technology is perhaps the best testimony of a positive CO_2 fertilizer effect in the greenhouse setting. Yield increases of 30–40% for some crops are not uncommon when CO_2 concentrations are maintained at three times ambient levels, i.e., near 1000 ppm (Wittwer, 1986). This is, of course, dependent on maintaining other environmental factors near the optimum for growth. It has been recognized

for some time that an increase in water and fertilizer applications is necessary to obtain maximum CO_2 benefits in greenhouses (Wittwer and Robb, 1964).

There are a number of reasons for the strong positive response to CO_2 in greenhouses, in addition to the optimum growth conditions and lack of weed pressure. One is that many greenhouse crops have an indeterminate growth habit, which, as discussed in Section II-C(i), may make them more responsive to CO_2 enrichment than most field crops (Kramer, 1981). Another factor to note is that greenhouses without supplemental CO_2 often have CO_2 concentrations that have been depleted to very low levels (200–250 ppm; Goldsberry, 1986), and so the response to CO_2 doubling is more dramatic than we should expect from a doubling of atmospheric CO_2 from current levels of about 350 ppm, Figure 8-1.

B. Controlled Environment Experiments

The vast majority of our quantitative information regarding plant response to enhanced CO_2 is based on experiments in which CO_2 concentration alone was varied, while water, nutrients, temperature, and pest pressure were maintained near optimum for growth. Exhaustive reviews of this scientific literature by Kimball (1983) and Cure and Acock (1986) reveal that, under these circumstances, a doubling of CO_2 from about 350 to 700 ppm increases the productivity of C3 and C4 crop plants about 33% and 10%, respectively, on average. This information has had a tremendous impact on current opinion regarding the magnitude of the CO_2 fertilizer effect, and has been used extensively in crop models (see Section V).

Although the reviews by Kimball (1983) and Cure and Acock (1986) of controlled environment experiments are extremely valuable references that consolidate much of our current understanding regarding CO_2 effects, reliance on their calculated crop averages for predicting yield response to climate change on a global scale is far from ideal. Crop productivity in the field is never controlled by any one environmental variable exclusively; under field conditions temperature, light, water, and nutrient supply, etc. will have an interactive effect on the plant response to atmospheric CO_2 concentrations (see Section IV). Also, there are crucial differences in environmental conditions between experimental growth chambers and greenhouses and the field situation (Table 8-2).

Since the early 1980s a number of CO_2-enrichment experiments have been conducted in the field using open-top canopy chambers. Results have been highly variable, but in general they have confirmed results obtained in more controlled environments. Substantial yield increases of C3 crops occur (e.g., 20–80%, depending on crop and specific conditions) when temperatures are not too low or too high, and adequate water and fertilizer are supplied.

Table 8-2. Environmental differences between controlled environments and the field.

Environmental factor	Controlled environment	Field
Light	1) Often low intensity	1) Very high intensity in sunlight
	2) Constant	2) Highly variable
	3) Spectral differences from daylight	
Temperature	1) Usually optimum or high	1) In temperate regions often suboptimal early and late in growing season
	2) Often constant during day and night	2) Very variable during the day/night cycle, and during the growing season
Light x temperature	1) Poorly coupled	1) Strongly coupled
Water	1) Often high humidity	1) Very variable humidity
	2) Low wind speed	2) Wind speed variable, can be very high
	3) Regular application in small amounts	3) Application very erratic, if at all
Nutrition	1) Regular application in small amounts	1) Few applications in larger amounts, if at all
Rooting volume	1) Very small	1) Large
	2) Often soil-less growing media	2) Soil type and depth varies

Adapted from Lawlor and Mitchell (1991).

The field studies with open-top chambers are an improvement over laboratory and greenhouse experiments in that the plants are exposed to natural light conditions, and there are more realistic day-night and short term variations in temperature and humidity. Nevertheless, the environment is altered. Compared to the open field, temperatures are often a few degrees warmer, wind and air mixing around the plant foliage are less, and pest pressure may be less because of isolation from the rest of the crop (Lawlor and Mitchell, 1991). These factors will affect growth, and, in fact, increases in

productivity due to the chamber effect alone have been reported. Open-top chambers *without* CO_2 enrichment increased the growth of soybean (Rogers et al., 1983) and maize (Rogers et al., 1986) compared to the open field.

Free-air CO_2 enrichment (FACE) is a relatively new approach for studies in the open field (Hendry, 1992). The technology for maintaining uniform CO_2 concentrations is still being tested, and few published results of crop response are available at this time. One preliminary study with cotton (Kimball, 1986b) found that, relative to a control at about 370 ppm CO_2, total yield increased 22% in a FACE treatment where CO_2 concentrations averaged about 1000 ppm in the morning hours to 500 ppm at midday. This yield response was less than the 50% increase reported for an open-top chamber treatment maintained near 650 ppm CO_2 in the same study.

IV. INTERACTIONS BETWEEN CO_2 AND OTHER ENVIRONMENTAL FACTORS

Plant growth is dependent on many factors in addition to CO_2, and if any one of these is in short supply, or at supraoptimal levels, growth will be slowed or plant survival itself may be jeopardized. The "principle of limiting factors" (Blackman, 1905) states that whichever factor is in shortest supply will be "limiting" and determine growth rate. We know that this model of plant response to the environment is simplistic, and there is reason to suspect that plant response to CO_2 may partially compensate for or exacerbate stresses associated with other factors. Also, it is unlikely that all plant responses to CO_2 would be limited by the levels of other environmental variables in exactly the same way. It is important that we learn to what extent yield response to CO_2, on both an absolute and relative basis, will be similar under stress compared to optimal environmental conditions.

The literature review by Cure and Acock (1986) found that data on interactions between CO_2 and other environmental factors were scarce and variable. They concluded that, until better quantitative information is available, prediction of response to CO_2 under specific environmental conditions will not be possible. Since that time, the USDA, EPA, DOE, and other agencies and research institutions have focused more attention on this issue. Our knowledge remains incomplete, but below we have attempted to describe some of the major findings regarding plant response to CO_2 in relation to changes in other biotic and abiotic factors controlling growth.

A. Temperature and CO_2

i. Photosynthetic Response

A strong interaction between temperature and photosynthetic response to CO_2 has been recognized for many years. At low temperatures there is little or no benefit from CO_2 enrichment, but as temperatures rise toward an optimum the proportionate stimulation of photosynthesis increases (Jolliffe and Tregunna, 1968; Berry and Björkman, 1980). The primary explanation for this is that the inhibitory effect of CO_2 on photorespiration (see Section II-A) increases with increasing temperature.

When plants have been acclimated to high CO_2 concentrations for some time, the CO_2 x temperature interaction becomes more complex and we may observe a *negative* effect from CO_2 at low temperatures. This is associated with the downregulation of photosynthesis phenomenon discussed in Section II-C(i), where the activity of the important photosynthetic enzyme, Rubisco, is reduced in plants exposed to high CO_2 for prolonged periods. When this occurs in CO_2-enriched plants whose photosynthetic biochemistry is also being slowed by low temperature, the result can be a *lower* photosynthetic rate than control plants.

The CO_2 x temperature interactive effect on photosynthesis is illustrated in Figure 8-2, which shows the photosynthetic response to temperature for control plants and for CO_2-enriched plants with and without an assumption of reduced Rubisco activity after acclimation to high CO_2 (Long, 1991). The benefit from increased CO_2 is much less at temperatures below 20° C than at warmer temperatures, even without an acclimation response. In simulations where it was assumed that acclimation to high CO_2 reduced Rubisco activity to 60 and 80%, the photosynthetic rate of CO_2-enriched plants became lower than the controls at temperatures of 22.5° and 12.5° C, respectively.

Another feature to note in the curves of Figure 8-2 is that the optimal temperature for photosynthesis is 4–5 degrees higher at the higher CO_2 concentration. Under some environmental conditions, this may compensate for the increase in leaf temperature that results from partial stomatal closure at elevated CO_2. An increase in leaf temperature will be of benefit for plants growing in an environment where air temperatures are below the photosynthesis optimum, but will have a negative effect when air temperatures are already high by shifting leaf temperature into the range where photosynthesis begins a sharp decline. Higher leaf temperatures resulting from CO_2 doubling could potentially place the crop productivity of more regions of the world in jeopardy from global warming than simply looking at air temperatures would indicate.
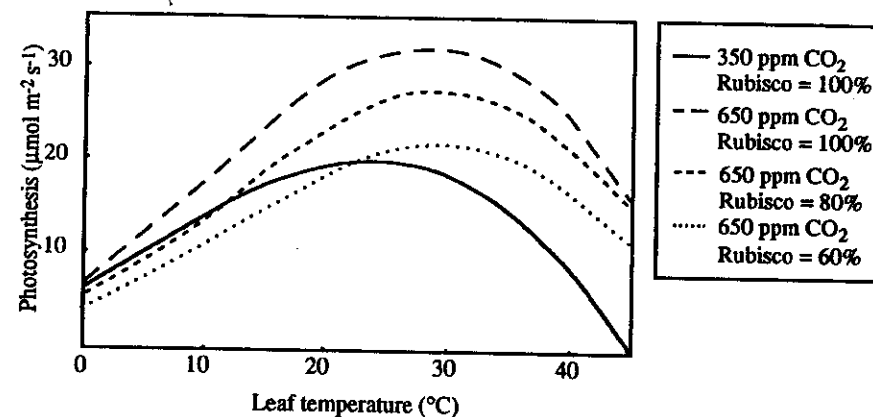

Figure 8-2. Photosynthesis per unit leaf area in relation to leaf temperature, CO_2 concentration, and activity level of the key photosynthetic enzyme, Rubisco. Plants at 350 ppm CO_2 are compared to plants at 650 ppm CO_2 with 60, 80 and 100% Rubisco activity levels. The reductions in Rubisco activity are observed in some species after prolonged exposure to high CO_2 concentration. Source: Long (1991).

ii. Plant Growth and Yield Response

Cure and Acock (1986) found some evidence to suggest that relative increases in plant growth due to CO_2 enrichment were generally greater at warmer temperatures. However, the studies reviewed were not specifically designed to investigate the temperature effect, and most involved only a narrow temperature range.

There is almost no information regarding the CO_2 x temperature interaction under field conditions. Little benefit from CO_2 enrichment was observed in natural tundra vegetation at a high latitude site with cool temperatures (Oechel and Reichers, 1987), whereas enrichment of warm wetland vegetation at a low latitude site produced significant increases in productivity (Drake and Leadley, 1991). Other factors, such as limited nutrient availability at the high latitude site, may also have been involved.

Idso et al. (1987) conducted a field study with open-top canopy chambers to examine the effect of temperature on weekly growth rates of five plant species grown with or without CO_2 doubling. The species were carrot, radish, water hyacinth, water fern, and cotton. All five species showed similar relationships between temperature and relative growth response to CO_2, despite their considerable genetic and morphological differences. The combined data were fitted to a single linear regression line as shown in Figure 8-3. The response to CO_2 enrichment ranged from a 60% *reduction* in growth

at 12° C, to no CO_2 fertilizer effect at 18.5° C, to relative growth increases of 30% at 22° C, and 100% at 30° C.

The implications of the study by Idso et al. (1987) are that the simplistic assumption of an approximate 33% increase in C3 crop yields with a doubling of atmospheric CO_2 may substantially underestimate the CO_2 fertilizer effect at warm temperatures, while overestimating the effect when average temperatures are below 20° C. The strong negative effect at temperatures below 18° C is of particular concern since, despite global warming, the 24-hour average temperature will be well below 18° C for much of the critical crop production period in many temperate regions of the world. Some climate models suggest that the temperature increases with global warming will be greatest in the winter in northern latitudes, rather than spring through fall when most crops are produced (Bretherton, 1990).

The results of Figure 8-3, based on a limited data set and a single research approach, cannot be viewed as conclusive. Subsequent experiments with carrot and radish (Idso and Kimball, 1989) found a threshold temperature at which high CO_2 became inhibitory of 12° C rather than 18.5° C, and there was less benefit at high temperatures for radish than indicated in Figure 8-3. The specific slopes and threshold temperatures will undoubtedly be modified as we gather information for more species and temperature regimes. Nevertheless, our understanding of the biochemical mechanisms underlying the photosynthetic response to CO_2 and temperature (Figure 8-2) suggests that a general trend similar to that shown in Figure 8-3 will be found for many important crop species.

Considering our relative certainty that changes in temperature will accompany predicted increases in atmospheric CO_2 concentration, it is surprising that the interaction between these two environmental factors has not received more attention. Research on this subject, particularly under field conditions, should be a high priority.

B. Water and CO_2

Although a global annual increase in precipitation is expected with a CO_2-doubling, conditions may be drier during the summer months for large portions of North and Central America, western Europe, central Asia, eastern Brazil, and north and western Africa (Parry, 1990). One analysis indicates that droughts may begin to increase in frequency in the 1990s, and by the 2050s, severe droughts may occur about 50% of the time compared to 5% of the time under the current climate (Rosenzweig, 1989). Shifts in precipitation patterns will have a substantial impact on agriculture. Dryland farming (reliance on stored soil water without supplemental irrigation) is still common for production of wheat and some other food staples in the developed world, and
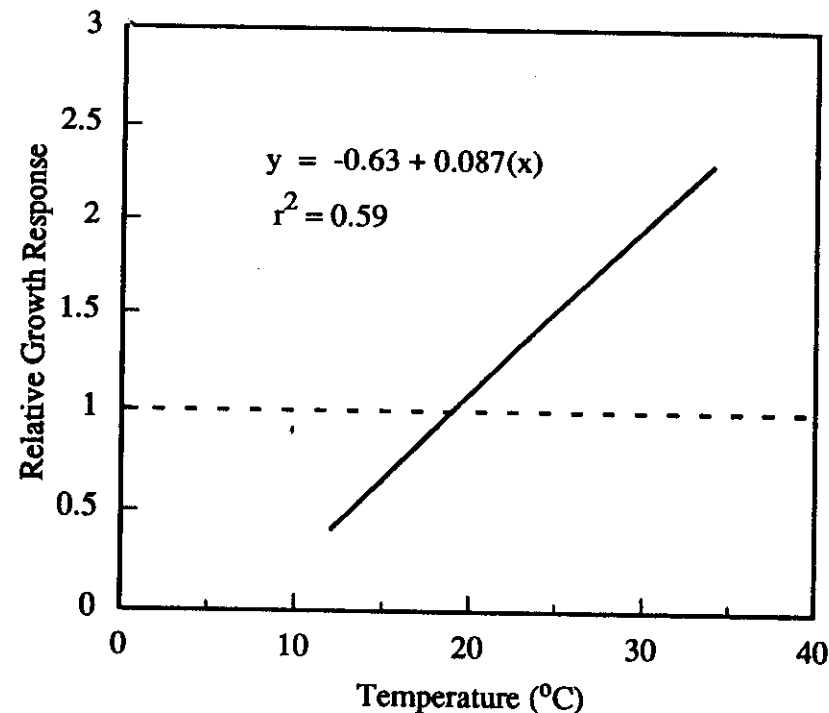

Figure 8-3. Relative growth response of plants to a 300 ppm increase in atmospheric CO_2 concentration in relation to average air temperature during the growth period. A value of 1.0 indicates no response to elevated CO_2, and values below or above 1.0 indicate negative or positive responses to CO_2, respectively. Results are based on data from five plant species. Source: Idso et al. (1987).

in most developing nations the majority of farmers do not have access to irrigation. These are compelling reasons for understanding the interaction between plant response to water stress and elevated CO_2.

The improved water use efficiency of CO_2-enriched plants may be of benefit under water-limited conditions (Section II-B). However, when CO_2 enrichment causes a larger leaf area and rooting volume, stored soil water can be depleted more rapidly despite a more efficient use of water, and this can lead to severe stress earlier in the plant life cycle than would occur without additional CO_2.

The results shown in Figure 8-4, published by Gifford (1979), are typical of many controlled environment experiments. A review by Kimball (1986a) concluded that, in general, the relative yield increase with CO_2 enrichment is
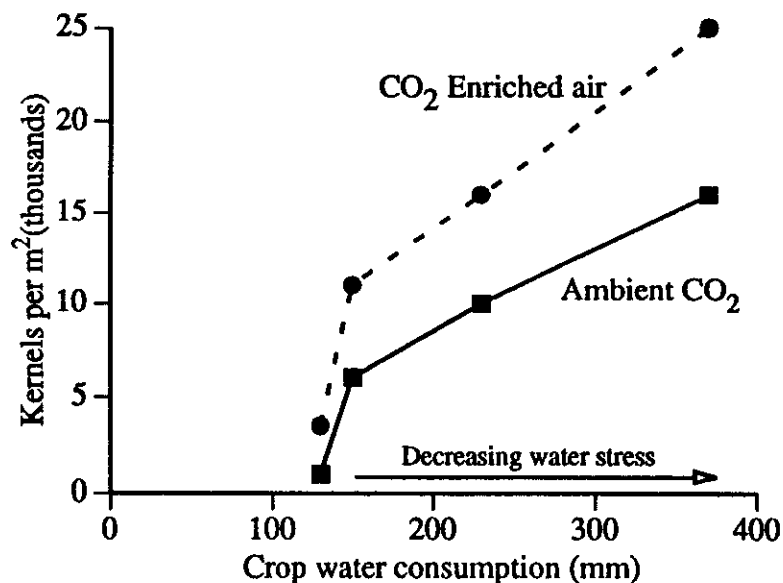
Figure 8-4. Yield response of wheat plants grown with or without CO_2 enrichment and exposed to various levels of drought stress. Increasing amounts of crop water consumption (i.e., transpiration) reflect increasing amounts of water applied and less plant water stress. Source: Gifford (1979).

as large or larger under water stress as under non-stressed conditions. Under some circumstances, the benefit from CO_2 enrichment may compensate for a *mild* water stress. However, under moderate to severe water stress, absolute yields are very low regardless of atmospheric CO_2 concentration, and the benefit from CO_2 enrichment is therefore minimal. This is illustrated in Figure 8-4, where the *relative* enhancement of yield by CO_2 enrichment increases with increasing water stress, but in *absolute* terms, yields are very low at both normal and enhanced CO_2 levels when water shortages become severe.

C. Nutrients and CO_2

The experience of commercial greenhouse producers, as well as CO_2 enrichment experiments, have demonstrated that the benefit from elevated CO_2 is much less when plant nutrients are in limited supply (Wittwer and Robb, 1964; Acock and Allen, 1985). Many investigations have focused on nitrogen and phosphorous, since these elements most frequently limit crop productivity. Wong (1979) grew cotton and maize in the greenhouse with varying nutrient solutions and found that the response to CO_2 was propor-

tionally smaller in low-nitrogen treatments. In contrast, field experiments with cotton (Kimball, 1986b) and rice (Allen, 1991) found that, on a relative basis, the response to CO_2 enrichment improved at low compared to high nitrogen levels. In all cases, however, maximum yields with CO_2 enrichment occurred when nitrogen fertility was optimal for growth. Goudriaan and de Ruiter (1983) compared the effects of nitrogen and phosphorous deficiencies and found that some small positive CO_2 response was maintained even at low nitrogen levels, but there was no CO_2 fertilizer effect when phosphorous was in short supply. The experiment by Goudriaan and de Ruiter (1983) also confirmed earlier findings of Wong (1979) that maize, a C4 species, is less able than C3 species to take advantage of CO_2 enrichment when nitrogen is in short supply.

We have very little specific information about essential plant nutrients other than nitrogen and phosphorous, and we know even less about the effect of CO_2 on soil microbial processes that may affect nutrient availability. Allen (1991) found that CO_2 enrichment had a positive effect on nitrogen-fixing bacteria in the soil, and this improved nitrogen nutrition and yield of rice plants. In contrast, elevated CO_2 had the negative effect of doubling the quantity of nitrogen, phosphorous, and potassium leached below the root zone in an artificial tropical ecosystem (Körner and Arnone, 1992). This may have been associated with a stimulation of soil microbial activity or a more rapid turnover of fibrous roots at the higher CO_2 concentration. An accurate assessment of the effects of CO_2-doubling on crop productivity will require more information regarding these complex interactions between CO_2 and nutrient availability, and a better understanding of how specific nutrient deficiencies influence plant response to CO_2.

D. Weed, Disease, and Insect Pests and CO_2

i. Weed Competition with Crop Plants

An increase in atmospheric CO_2 will of course affect weed species as well as commercially important crop plants. Unfortunately, essentially all of our information regarding crop response to CO_2 is based on experiments in which competition from weeds was not a factor. Wittwer (1990) suggested that the rising CO_2 levels will generally favor crop production since the majority of our important food crops have the C3 photosynthetic pathway, while a high percentage of the major weed pests are C4 plants that will likely benefit less from CO_2 enrichment. This overlooks the fact that even an optimistic 30% increase in growth of C3 crops will not be sufficient to overcome the existing growth rate and competitive ability of some C4 weeds. Also, important C4 crops, such as maize and sugarcane, may experience yield reductions because

of increased competition from C3 weeds. It should be noted that maize accounts for about 75% of all traded grain and is the major grain used in food relief programs in famine-prone regions (Parry, 1990).

Broad generalizations regarding CO_2 enrichment effects on crop-weed competition provide little insight into the specific weed control challenges that farmers will have to face in the coming century. The site-specific mix of weed and crop species, and the relative response of each of these species to environmental conditions in the future CO_2-rich world, will determine the economic outcome for both farmers and consumers.

ii. Disease and Insect Pressure

Evidence that the protein concentration of plants may be reduced as a result of increased CO_2 (Parry, 1990) implies not only lower nutritional value for human consumption, but also for leaf-feeding insects. This may induce greater insect mortality, but surviving insects could consume more foliage to compensate for poorer quality food (Fajer, 1989). Natural selection would tend to favor the evolution of insect genotypes that consume more plant material more rapidly. Bazzaz and Fajer (1992) suggested such augmented consumption by insects could negate any benefit gained from the hypothesized crop yield boon in a CO_2-rich environment (p. 72).

The climate changes that result from increased atmospheric CO_2 concentrations will undoubtedly influence the geographic range of insect and disease pests. Warmer temperatures in high latitude areas may allow more insects to overwinter in these areas. Also, crop damage from plant diseases is likely to increase in temperate regions because many fungal and bacterial diseases have a greater potential to reach severe levels when temperatures are warmer or when precipitation increases (Parry, 1990).

E. Air Pollutants, Ultraviolet (UV) Radiation and CO_2

i. Air Pollutants

The burning of fossil fuels, which is the primary cause of increasing atmospheric CO_2 concentrations, also introduces into the atmosphere several air pollutants or their precursors. The three air pollutants that cause the greatest damage to crops are ozone (O_3), sulfur dioxide (SO_2), and nitrogen dioxide (NO_2). Of these, O_3 probably has the greatest economic impact. Estimated yield losses at a 7-hr/day average O_3 concentration of 0.09 ppm are 12.5%, 30.7%, and 27.4% for corn, soybean, and wheat, respectively (Heck et al., 1984). The national composite average of O_3 (measured as second-highest daily maximum at 471 sites in the U.S.) crossed the 0.12 ppm mark in 1991

(U.S. EPA, 1991). Estimation of actual U.S. financial losses due to O_3-related yield reductions range from $1–5 billion per year (Fishman, 1990). The effects of SO_2 and NO_2, and resulting acid rain and dry deposition on crop yields, are less definitive and can have both positive and negative impacts. On the positive side, both nitrogen and sulfur are essential elements in plant nutrition, so that additions to the soil or leaves may benefit plant growth if these elements are in short supply. The negative effects include reductions in photosynthetic rate (Allen, 1990), reduced plant resistance to pathogens, and soil acidification (Canter, 1986). There is some evidence of a synergism between SO_2 and NO_2, such that the negative effect of each pollutant is greater when both pollutants are present (Carlson, 1983).

Since increased CO_2 concentrations cause partial stomatal closure, and most air pollutants enter the plant through the stomates, there is reason to believe that a CO_2 doubling will tend to lessen the yield reductions due to air pollutants. This does appear to be the case for some species, although CO_2 enrichment has seldom been found to completely overcome the adverse pollution effects. Elevated CO_2 concentration reduced O_3 leaf damage by 14% in bean and 66% in tobacco (Heck and Dunning, 1967). Leaf injury caused by SO_2 was reduced 60% at high CO_2 levels in another study (Hou et al., 1977). Allen (1990) used a simple model to show that stomatal closure with a CO_2 doubling could theoretically reduce the damaging effects of O_3 and SO_2 by 15%. Such partial alleviation of pollution stress by high CO_2 may not occur in all species. Carlson and Bazzaz (1982) found that several C4 species had the opposite reaction from the one described above for C3 crops. In their study, C4 plants exposed to SO_2 had reduced growth at high CO_2 concentrations, but not at 300 ppm CO_2.

The research conducted thus far indicates that the crop yield response to air pollutants in a CO_2-enriched world will depend on three key factors: (1) the concentration and potential toxicity of the air pollutant; (2) the degree to which partial stomatal closure limits contact of plant tissues with the pollutant; and (3) the relative magnitude of direct CO_2 effects on photosynthesis and plant growth. These factors will vary with the particular air pollutant, the CO_2 concentration, crop species and growth stage, and environmental factors.

ii. UV Radiation

Two trace gases contributing to global warming, the chlorofluorocarbons (CFCs) and oxides of nitrogen, also are associated with the degradation of the stratospheric ozone layer (at a rate of 3–5% per decade (Kerr, 1991)), and this is increasing the flux of UV radiation to the earth. An increase in UV radiation is not only a direct threat to human health, but also has a negative impact on photosynthesis and growth of many plant species. Approximately 300 plant species and varieties have been studied to date, and of these about half show

physiological damage or growth reductions in response to UV radiation (Teramura, 1990). Many important crop species respond negatively, including maize, potato, soybean, tomato, cabbage, and squash. Results have been highly variable, dependent on environment and the particular variety used. Multi-year field studies measuring yield are scarce, but one such study with soybean found a 20–25% yield reduction in 4 of 6 years with UV-B radiation levels simulating a 25% ozone depletion (Teramura, 1990).

The CFCs released into the atmosphere remain active for many years, so that even as CFC production decreases because of new regulations, UV radiation levels are anticipated to continue rising well into the next century. For this reason, an understanding of the interaction between plant response to UV and CO_2 concentration will be important. Ultraviolet radiation affects a number of plant biochemical processes directly associated with photosynthesis and pigment formation, and also affects leaf morphology and biomass partitioning (Teramura, 1990). These effects are likely to alter plant response to CO_2, but at present we have essentially no information regarding this issue.

V. CROP MODELS AND THE CO_2 EFFECT

Some climate change researchers, such as Kaiser et al. (Chapter 7) do not include a CO_2 fertilizer effect in their crop growth models because of the many uncertainties involved. This is the exception; based primarily on data from controlled environment experiments conducted under optimum growing conditions, most modelers have incorporated global multipliers or yield shifts that assume very positive benefits from increased CO_2. The examples that follow illustrate the types of basic assumptions employed, and the impact these assumptions have on yield and economic welfare predictions.

A. Model Assumptions

i. Magnitude and Direction of the CO_2 Effect

Typically in climate change studies, temperature, precipitation, and other output from GCMs are used as input for the crop growth models. This can lead to an error in CO_2 concentrations assumed because the GCMs generate data based on an "*equivalent* CO_2 doubling," which includes the radiative forcing effects of various trace gases as well as CO_2. Trace gases may account for as much as 39% of the human-related forcing (Houghton, 1990). Under these circumstances, atmospheric CO_2 concentrations would be closer to 550 ppm at the time of equivalent CO_2 doubling rather than the 660 ppm (2 x 330) used in most CO_2 enrichment experiments and assumed in many crop models incorporating a CO_2 fertilizer effect.

A recent study by Rosenzweig et al. (1992) (Chapter 5) attempted to correct for this by estimating photosynthetic rates at 555 ppm CO_2. Their CO_2 fertilizer assumptions were nevertheless optimistic since they were based primarily on data from Cure and Acock (1986) and Kimball (1983), which summarize results from controlled environment experiments conducted under optimum growing conditions (see Table 8-2 and discussion in Section III-B). The 555 ppm CO_2/330 ppm CO_2 photosynthesis ratios used by Rosenzweig et al. were 1.21, 1.17, and 1.06 for soybean, wheat and rice, and maize, respectively. The authors indicated that this "... may overstate the positive effects of CO_2, because uncertainty exists concerning the extent to which the beneficial effects of increasing CO_2 will be seen in crops growing in variable, windy, and pest-infested (weed, insects, and diseases) fields under climate change conditions" (Rosenzweig et al., 1992, p.3).

In the MINK study (Chapter 6), Easterling et al. (1992) adopted the concept of radiation-use efficiency (RUE), which is the amount of biomass (i.e. total plant dry weight) produced per unit of incoming light energy. They then used the same Kimball (1983) data set utilized by Rosenzweig et al. (1992) and other groups to generate a curve predicting the increase in RUE with increases in CO_2 concentration. The RUE optimistically was assumed to increase 10%, 24%, and 33% with CO_2 doubling for maize, soybean, and wheat, respectively.

ii. Environmental and Economic Constraints

a. Environmental Factors

Most climate change research is focused on the effects of global warming, so modelers have focussed their attention on plant response to temperature. However, to our knowledge, the well-documented interaction between temperature and CO_2 illustrated in Figures 8-2 and 8-3 (Section IV-A) has not been incorporated into any of the models currently used in climate change studies. The CO_2 fertilizer effect is applied as a constant multiplier, independent of day-night and seasonal temperature fluctuations. The CO_2 fertilizer effect is always assumed to be positive, even when modeling within the low temperature range of 10–20° C, where all experimental evidence indicates the effect becomes relatively small or even negative. The robust and well-tested photosynthesis models that describe the underlying mechanisms of the CO_2 x temperature interaction (Long, 1991; Farquhar, 1980) have not been incorporated into crop models used in climate change research.

Several existing crop models have the capacity to simulate the supply-demand balance for water and nutrients. For the MINK study (Easterling et al., 1992; Chapter 6) nutrients were assumed non-limiting, but simulations with and without irrigation were conducted utilizing the water balance

component of their crop model. They also added a linear function that predicts a 60% reduction in stomatal conductance (i.e., partial stomatal closure) with a doubling of CO_2. Although this function is based on controlled environment experiments and results in quite optimistic forecasts of water use efficiency at higher CO_2 concentrations, it is a step forward in terms of incorporation of well-established CO_2 x environment interactive effects.

Crop models used in Rosenzweig et al. (1992; Chapter 5) can predict crop growth as influenced by temperature, precipitation, and management practices such as irrigation and fertilizer application. The models were not modified to incorporate possible interactive effects, but crop yield predictions with and without irrigation and additional fertilizer were compared in their simulations.

To date, little effort has been made to incorporate the effects of weed, insect, or pest pressure, or effects from air pollutants and UV radiation, into crop models used in climate change research. These effects may completely negate any possible benefits from CO_2 enrichment. More research is needed to quantify these effects, and to quantify the interaction between plant response to these environmental factors and CO_2, so that the yield predictions for a CO_2-doubling become more realistic.

b. Economic Issues

The majority of the published literature on predicted crop response to climate change has assumed a maximum CO_2 beneficial effect, and most researchers agree that this would require an increase in water, fertilizer, and other inputs. Little effort has been made to determine whether increasing these expensive inputs in proportion to increases in CO_2 levels will be economically optimal. Also, the assumption has usually been that additional resources will be made available as needed, and as crop production zones shift. The reality is that the availability of water and other critical resources is extremely difficult to predict, and these resources may be in short supply in many underdeveloped as well as developed nations. Resource conservation and concerns regarding environmental impact are other factors that will constrain the use of increased amounts of water, fertilizer, and pesticides. The economic analysis by Rosenzweig et al. (1992; Chapter 5) and a recent review by Bazzaz and Fajer (1992) concluded that the poorer, underdeveloped nations will be at a greater disadvantage in a CO_2-rich world than they are today because of their limited ability to supply the inputs necessary for realization of the CO_2 fertilizer effect.

B. Sensitivity of Economic Forecasts to the CO_2 Effect

Rosenzweig et al. (1992; Chapter 5) found that, without the direct CO_2 fertilizer effect, forecasted crop yields were reduced due to climate change in all countries and GCM scenarios investigated. When the CO_2 fertilizer effect was incorporated, many of the crop yields increased, and all significantly improved. Economic analyses and analyses of risk from hunger were all based on yield forecasts that assumed a strong CO_2 fertilization effect.

Adams et al. (1990) reported that using the Geophysical Fluid Dynamics Laboratory (GFDL) model, for a doubling of CO_2, the impact of climate change on U.S. economic surpluses went from a negative $35.9 to a negative $10.5 billion, without and with the CO_2 fertilizer effect, respectively. Forecasts using the Goddard Institute of Space Studies (GISS) model showed that inclusion of the CO_2 fertilization effect converted a *negative* $6.5 billion change in economic surplus to a *positive* $9.9 billion change.

Easterling et al. (1992; Crosson, Chapter 6) modeled the CO_2 fertilizer effect alone as responsible for a 58% increase in value of production with the worst case scenario of no on-farm adjustments to climate change. In a scenario assuming use of adaptation technology, a positive CO_2 fertilizer effect shifted total forecasted *losses* of $2.03 billion to total *gains* of $645 million.

These results indicate why a critical analysis of the approach to modeling CO_2 effects is in order. As emphasized by Erickson (1993), regional, national, and even global agricultural and climate change policies may become dependent on the magnitude assigned to this one variable.

VI. SUMMARY

Most of our information regarding plant response to CO_2 is derived from controlled environment experiments where water and nutrients were in adequate supply, temperatures were near optimum, and weed, disease, and insect pests were not present. Under these circumstances, many C3 species (includes wheat, rice, soybean, and certain weeds) show a significant increase in photosynthetic rate and water use efficiency per unit leaf area at high CO_2 concentrations. Plant growth and yield may increase by as much as one-third with a doubling of CO_2. The C4 species, including the important crop plants maize, sugarcane, millet, and sorghum, usually show relatively little benefit from increased CO_2.

However, when plants grow in a field situation, the optimum conditions required for full realization of the benefits from CO_2 enrichment are seldom, if ever, maintained. This is particularly true for natural ecosystems and for agricultural ecosystems in underdeveloped countries where irrigation, fertil-

izer, herbicides, and pesticides are not available or are prohibitively expensive. Even in developed countries, the increase in water, nutrient, and chemical inputs necessary for maximum CO_2 benefit may not be cost-effective or may be limited by concerns regarding resource conservation or environmental quality. In some regions, the potential benefits from CO_2 may be negated by other factors associated with climate change, such as crop damage due to increases in air pollutants or UV radiation.

The specific temperature range for realization of a positive CO_2 effect will undoubtedly vary among crop genotypes, but we know that for most crops the lower temperature limit is somewhere between 10° and 20° C. This has important implications for many temperate regions of the world where, despite global warming, average temperatures during early and late portions of the growing season will be suboptimal and little benefit from a CO_2 doubling, or even a negative growth response, may occur.

In a recent review, Cline (1992) concluded, "It would seem risky to count on agriculture in general experiencing the same degree of benefits from carbon fertilization as has been observed in the laboratory experiments, especially in developing countries where the complementary water and fertilizers may be lacking" (p. 91). Nevertheless, most of our information is from controlled environment studies, and crop modelers have relied on these data for determining the magnitude of their CO_2 fertilizer variable. Some models are capable of separately simulating water and nutrient limitations, but yield and economic forecasts usually assume these growth factors are non-limiting. The many complex interactions between CO_2 and other environmental variables have, for the most part, not been incorporated into crop models used in climate research. Below are some specific suggestions for modeling and interpreting the CO_2 fertilizer effect:

1) Given the uncertainties regarding resource availability and crop response to CO_2 in a future CO_2-rich environment, a conservative policy approach would be to assume no CO_2 fertilizer effect. This may be particularly appropriate for some natural ecosystems and agricultural ecosystems in underdeveloped countries. For policy analysis, modelers should provide results without, as well as with, the CO_2 fertilizer effects. An effort should be made to incorporate economic and resource constraints into crop models as modifiers of the CO_2 variable.

2) The CO_2 x temperature interaction illustrated in Figs. 8-2 and 8-3 (Section IV-A) should be determined for major food crops and a wide temperature range, and incorporated into crop growth models. In the interim, it may be more accurate to assume no CO_2 fertilizer effect at suboptimal temperatures (e.g., less than 15° C).

3) The increase in leaf temperature at increasing CO_2 concentrations can be incorporated into crop models using existing leaf energy balance equations. Leaf temperature could then be linked to plant water use and photosynthesis components of growth models.

4) More field research investigating other environment x CO_2 interactions will be necessary to improve the accuracy of economic forecasts.

5) More information is needed regarding the effects of CO_2-doubling on competition from weeds, and damage from insect and disease pests.

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